Pestic. Sci. 1997, **51**, 299–304

Phenological Adaptation in Weeds—an Evolutionary Response to the Use of Herbicides?*

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(Received 1 May 1997; revised version received 16 July 1997; accepted 31 July 1997)

Abstract: The possibility of phenological adaptation in weed species is discussed in terms of an evolved response to herbicide use. Weed populations often exhibit heritable variation in life history traits that may reflect phenological adaptations. Approaches to assessing 'adaptedness' are discussed. Selection for seed dormancy in a grass weed is considered through life history analysis. It is concluded that too little is known about both life histories and fitness of weed species in varying environments for conclusions to be drawn concerning phenological adaptation for use in herbicide resistance management.

Pestic Sci., **51**, 299–304, 1997
No. of Figures: 2. No. of Tables: 2. No. of Refs: 38

Key words: life history, phenology, fitness, heritability, weeds

1 INTRODUCTION

Phenology is defined botanically as the periodically changing form (seedling, vegetative or adult) of a plant as this affects its relationship with its environment.[1] Ever since the wide-scale adoption of herbicides for weed control, the proposition that weed species may evolve phenological adaptations in response to herbicide use has been raised periodically in the literature.[2–4] More recently, there have been calls for analysis of the durability of integrated weed-management systems (employing multiple control measures) through assessment of the evolutionary responses or adaptations that may occur in the weed flora.[5] Moreover it has been suggested that herbicide-resistant *Lolium multiflorum* Lam. in wheat may be managed through manipulation of patterns of selection for germination response by altering cropping practices.[6] Understanding the potential for, and likely speed of, evolutionary change in weed populations is clearly of importance if sustainable weed management practices are to be advocated to farmers. This paper considers the question 'other than in expressing herbicide resistance, do weed species adapt to herbicides by phenological changes?'

* Based on a presentation at the Conference 'Resistance '97—Integrated Approach to Combating Resistance' organised by the Institute of Arable Crops Research in collaboration with the SCI Pesticides Group and the British Crop Protection Council and held at Harpenden, Herts, UK on 14–16 April 1997.

2 PHENOLOGICAL ADAPTATION

In discussing the possibility of phenological adaptation as an evolutionary response, it is useful to distinguish between *adaptive*, defined as conferring a benefit on an organism with regard to its present relationship with its environment,[7] and *ad* (or *ab*[8]) *-apted*, which describes a trait that is presumed to be the product of natural selection over past generations and has become fixed by selection. Thus, *adapted* refers to the causal origin of a trait in evolutionary history whereas *adaptive* describes the present value of a trait in a given environment.

Individuals of all higher plant species undergo changes in life form or phenology as a consequence of development from the zygote and in the expression of modular plant growth.[9] Intrinsically, the rate of this development and expression is influenced by environmental factors. However, the phenotype of the individual is not a fixed suite of morphological and physiological characteristics programmed by specific

unitary genes, but is a consequence of the interaction of a genetically determined developmental programme (the genotype) with an environmental experience throughout the life of the organism. Bradshaw[10] points out that 'the way in which a plant reacts to different environments is as much a part of its characteristics as its appearance and qualities in a single environment'. Phenotypic plasticity, is then the term used to define the degree to which phenotypic expression of a genotype varies under different environmental conditions and an individual's range of phenotypic responses is its 'norm of reaction'.[11] Variability in phenology at the individual plant level is therefore a component of phenotypic plasticity.

Weed species are frequently referred to in the literature as *plastic*, sometimes with ambiguous definition. However, the ability of a species to be plastic—to survive and reproduce in a wide range of environments—may be conferred by inter- and intra-population genotypic variability amongst individual plants, as well as by the adaptive nature of phenotypic plasticity itself. These means are not mutually exclusive and critical experimentation has exposed the considerable variation in degrees of inter- and intra-population variation and norms of reaction of individual genotypes in weed species.[4,12–14] Phenological adaptation in a species may therefore arise at various levels within a population.

Comparisons of herbicide-resistant and -susceptible biotypes in particular have shown that populations vary both in relation to morphological traits (leaf shape and angle, hairiness) as well as developmental responses (relative growth rate, competitive ability, photosynthetic rate, germination rate).[13,15–17] Seed germination polymorphisms are also characteristic of many weed species as a general adaptation to disturbed environments and inter-population variation in predictive (innate) and consequential (induced, enforced) dormancy is common.[3] Seed dormancy enables seed banks to persist such that ephemeral species may respond ecologically to herbicides without any evolutionary responses. For example, susceptible biotypes of *Senecio vulgaris* L. in soft fruit plantations in the UK which are under recurrent exposure to triazine herbicides occupy a winter annual niche as opposed to the normal spring and summer one.[18]

3 APPROACHES TO STUDYING ADAPTATION

One of the most potent environmental changes experienced by populations of a weed species is the net effect of weed management practices that result in mortality of individuals and the reduced fecundity of survivors. Weed management practices will, therefore, constitute agents of natural selection given heritable genetic variation for life-history traits in weed species. Populations may become adapted in that individuals possess adaptive traits as a consequence of past selection.

Jordan and Jannink[5] have itemized the components of the research program necessary to investigate the likelihood of adaptation in a weed species in response to control measures. It involves measurement of the effects of individual selection agents on the fitness (survivorship and seed production) of individuals classified by phenotypic variant (or ideally genotype) in contrasting environments. Given demonstrable differences in fitness, the genetic basis of variance and co-variance in traits influencing fitness is then investigated using quantitative genetical methods.[19] Finally, approaches such as multivariate selection analysis[20] may be used to determine the rate at which weed control measures may select for adapted genotypes. Jordan[21] provides an example of the approach.

There have been very few documented observations of actual responses in weed species to selection as a result of agricultural practices. For example, herbicide resistance in field populations is typically suspected, and if confirmed, analysed retrospectively. However, in the case of seed dormancy in wild oats (*Avena fatua* L.), Jana and Thai[22] investigated the change in frequency of dormant and non-dormant genotypes in relation to cropping practice over a period of seven years. Prior work had demonstrated genetic control of dormancy. In populations comprising equi-proportional mixtures of dormant and non-dormant pure lines at the start of the experiment, non-dormancy was maintained by continuous cropping but declined to a very low frequency where a summer fallow was imposed.

Experimental methods for studying adaptation in weed populations as just described are not only laborious, not least for the need to produce pure lines for comparative purposes, but also time-consuming to complete. Similarly, rigorous evolutionary analysis as illustrated by work on weeds of arable crops[21] and grassland,[23] respectively, requires a substantial breeding programme which, in practice, may be constrained by the breeding characteristics of a species. In consequence, it has been argued that comparative life-history analysis of intra-specific variation is an alternative approach in the assessment of adaptation.[24] Here, the performance of phenotypically variant populations, or progeny of individuals, is compared in selected common environments and, where appropriate, under reciprocal transplant (environmental) conditions. Typically, traits relating to fitness or survivorship, to reproduction and reproductive output themselves are measured. A criticism of this approach is that the observed phenotypic responses may be non-adaptive.[25] However, hypotheses may be raised concerning possible adaptations given interpretation of heritability of fitness traits within populations. From comparative analysis, populations exhibiting superior performance and an absence of additive genetic variation may be inferred to be adapted

to a given environment. Table 1 provides examples of life history or phenological traits in populations of some weed species that have been shown to be heritable. Heritability (intra-class correlation, narrow-sense heritability[19]) was measured by workers in various ways through reciprocal transplant experiments, common garden trials or genetic analysis. These studies demonstrate that populations of weed species vary in the levels of additive genetic variation, phenotypic variance being fixed in some populations or potentially responsive to selection in others.

4 SELECTION FOR DORMANCY IN RESPONSE TO HERBICIDE—A THEORETICAL INVESTIGATION BY LIFE-HISTORY ANALYSIS

Selection for seed dormancy may be postulated as an adaptive response to herbicide application in weed species showing episodic germination from a short-lived seed bank. In blackgrass, *Alopecurus myosuroides* (Huds.), an annual grass weed commonly associated with autumn-sown cereal crops in the UK, cohorts of seedlings may be recruited into an autumn-sown crop for several months extending into spring. Thus, seedling populations may span the time when post-emergence herbicides may be applied. The phenylurea herbicides, chlorotoluron and isoproturon, have been used extensively in weed control and the history of the occurrence and spread of herbicide resistance to blackgrass has been well documented.[26,27]

To examine fitness in resistant (R) and susceptible (S) biotypes of blackgrass, field plots (1·5 × 1·5 m) of winter wheat (*Triticum aestivum* L. cv. Avalon, sowing rate 375 kg ha^{-1}) were sown separately with 100 seeds m^{-2} of each biotype, in October 1985. The R biotype, which exhibits high resistance to phenylurea herbicides, was collected from Peldon, Essex, UK and the S biotype was the susceptible Rothamsted reference stock.[26] Emerging blackgrass plants were ringed at two-to-three-week intervals from early November 1985 and their fate recorded until crop harvest in August 1986. At harvest, spike lengths of individual reproductive tillers were recorded for all plants and a stratified number of spikes retained to calculate the allometric relationship between spike length and seed number. Plots were either sprayed or unsprayed in a factorial replicated design. The two post-emergence herbicides chlorotoluron and isoproturon were applied individually at rates of 2·75 and 2·1 kg ha^{-1} in 400 litre ha^{-1} of water, respectively, to each biotype in early March 1986. Details of the experimental and cultural methods followed are published elsewhere.[28]

Figure 1(a) illustrates the pattern of emergence of seedlings of the unsprayed S biotype, together with the likelihood of death before seed production (q_x) and the mean number of seeds produced per surviving plant (m_x). Mortality of plants was only evident in late-emerging cohorts of plants which were also less fecund than plants emerging earlier in the season. The corresponding patterns of survivorship and seed production according to time of emergence are given in Figs 1(b)

TABLE 1
Examples of Weed Species Exhibiting Heritable Variation in Life-History Traits[24]

Species	*Character*	*Degree of genetic control (t = intraclass correlation coefficient h² = heritability)*	*Distribution of variation intra- or inter-population*
Avena fatua[33,34]	Days of flowering	t = 0·40–0·75	Intra
	Tiller number	t = 0·15–0·34	
	Height	t = 0·22–0·61	
	Seed number	t = 0–0·28	
	Seed dormancy	h^2 = 0·5	
Lolium multiflorum[35]	Days to flowering	t = 1·89	Intra
	Height at maturity	t = 0·78	
Poa annua[36]	Pre-reproductive time	t = 0·48	Intra
		t = 0·21	Inter
	Plant diameter	t = 0·25	Intra
		t = 0·20	Inter
	Age-specific reproduction	t = 0·15–0·52	Intra
		t = 0·05–0·26	Inter
Oryza perennis[37]	Seedling survivorship	t = 0·3	Inter (annual,
	Adult survivorship	t = 0·37	perennial, and
	Seed bank (no. of		intermediate forms)
	viable buried seed)	t = 0·21–0·43	
Sinapis arvensis[38]	Seed dormancy	h^2 = 0·13	Intra

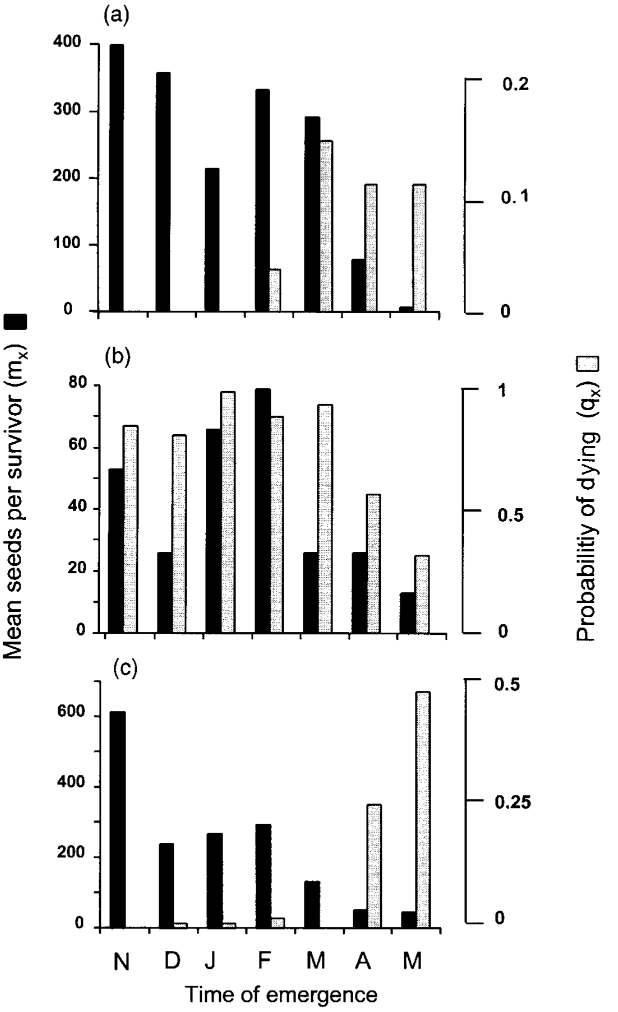

Fig. 1. Mortality and seed production in *Alopecurus myosuroides*. (a) S biotype, unsprayed; (b) S biotype, sprayed with chlorotoluron; (c) R biotype, sprayed with chlorotoluron.

and (c), respectively, for both biotypes in response to chlorotoluron. Chlorotoluron caused high mortality in all cohorts of the S biotype except those emerging after March. In contrast, the R biotype showed little mortality except in the last two cohorts. Seed production of surviving R plants was highest in the oldest plants (November cohort), plants emerging before spraying in December, January and February producing fewer seeds and at least three-fold more than S counterparts under herbicide treatment. Figure 1(b) illustrates that biotype fitness (the product of $1 - q_x$ and m_x) under chlorotoluron treatment is higher for the S biotype in plants emerging from February onwards, whilst in the R biotype, highest fitness accrues from early emergence. These data may be used to investigate the hypothesis that herbicide application may select for seasonal dormancy in the S biotype, given that dormancy is a heritable trait, and in the absence of resistance evolution.

The seed population size of *A. myosuroides*, after a generation of growth (N_{t+1}) is the result of contributions of seeds from plants emerging before spraying and those afterwards, assuming no carryover of seeds from previous generations. Thus, a difference equation can be written in the form

$$N_{t+1} = R_B(pN_t) + R_A(qN_t) \qquad (1)$$

where N_t is the seed population size in generation t. R_B is the contribution to the net rate of increase of plants that emerged before spraying (conventionally equivalent to $\sum l_x m_x$ for those cohorts, $l_x = 1 - q_x$) and R_A is the corresponding contribution of cohorts emerging after spraying; p is the proportion of every seed crop emerging before spraying and $q(= 1 - p)$ is the proportion emerging after spraying. The ratio p/q is assumed to be heritable and to respond to selection. The proportion of blackgrass seeds lost in the fallow period from summer seed shed to start of autumn seedling emergence is assumed to be constant for each biotype and is subsumed within R_A and R_B.

By iterating this equation, the fitness of individual biotypes may be compared for particular combinations of p and q, where R_A and R_B express the net outcome of all environmental conditions experienced by plants in respective groups. Estimates of R_A and R_B for R and S biotypes are given in Table 2 for three spraying regimes. Equation (1) was iterated for three generations (starting population size 10 seeds m^{-2}), randomly sampling

TABLE 2

Mean Relative Contributions ($\sum l_x m_x$) to *Alopecurus myosuroides* Population Growth Rate[a]

Treatment	*Rate (kg AI ha^{-1})*		*Cohort contributions to growth rate (seeds m^{-2})* — *Before spraying*	*After spraying*
Unsprayed	—	R	586	472
		S	971	637
Chlorotoluron	2·75	R	1079	443
		S	16	32
Isoproturon	2·1	R	94	5
		S	25	0·4

[a] See Section 4 for details.

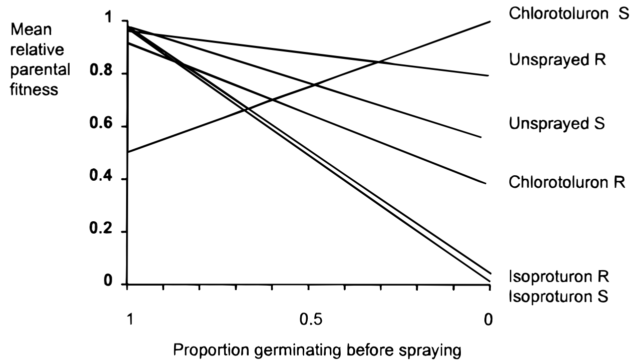

Fig. 2. Changes in parental fitness with change in the proportion of *Alopecurus myosuroides* seeds germinating before or after spraying herbicide (see Section 4 and Table 2 for details).

parameter values for R_A and R_B from normal distributions based on 95% confidence limits around each mean. Standard errors of means (not given) fell in the range of 11 to 22% of the means. N_{t+3} was used as a measure of fitness for phenotypes with particular combinations of p and q and relative parental fitness calculated as a ratio of the maximum phenotype performance. For all cases examined but one, the model indicates that there is no selective advantage in delaying germination until after spraying (Fig. 2). Only in the case of the S biotype when sprayed with chlorotoluron was relative parental fitness increased by delayed germination, reflecting the increased fitness of late emerging plants (Fig. 1(b)).

5 CONCLUSIONS

Herbicide resistance evolution itself clearly indicates the strength of directional selection that may occur, particularly where few loci are involved in the expression of functional resistance.[29] Contrastingly, adaptations through altered life history are likely to invoke multiple traits and evolutionary responses may be slower as multiple loci are involved, particularly where genes have pleiotropic and epistatic effects.

Early events in the life cycle of an annual weed, such as germination and establishment, often determine fitness. Modern herbicides exert greatest effect on plant mortality and selection to escape unfavourable periods for germination and establishment will be high. Late germination that results in escape from the risk of high mortality due to pre-emergence or early post-emergence herbicides places plants in a subordinate position in the size hierarchy of crop and early-germinating weeds. Later germination in consequence carriers with it the likelihood of lowered seed output whereas early germination has a high risk of mortality but higher reproductive output. The net result of these conflicting demands is a life history trade-off, later germination favouring the survival component of fitness and early germination favouring the reproductive component. Where herbicides exert variable selection, (intensity and direction) weed species may never show specific adaptation other than to a varying environment in which mortality is high. Clearly episodic emergence is a potential adaptation. The life-history analysis of *A. myosuroides* may be criticised on many grounds, including ecological simplicity and the use of a single set of fitness parameters so that, at best, it provides an example of the approach. However, it does strongly suggest that there is greatest advantage in early germination simply because of the high reproductive potential in a competitive crop-plant community. Whether this is truly adaptive is unclear, as the nature of heritable variation in seed dormancy in this species is unknown.

Phenological adaptation in weed species as an evolutionary response to herbicides remains a largely unexplored subject. It will remain so until fitness parameters are measured in more detail in response to herbicides and in field populations of weed species.[17] As an option for use in herbicide resistance management, however, little comment can be added to that made by previous authors,[5,30] as it will only be through critical and rigorous experimentation, with the often-reported associated logistical difficulties,[31] that the potential may emerge. This will necessarily need to focus on early demographic events in the evolutionary process and not least the importance of small population size.[32]

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